Nest distribution shaping within-stream variation in Atlantic salmon juvenile abundance and competition over small spatial scales

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Summary

1. Spatial heterogeneity in population density is predicted to have important effects on population characteristics, such as competition intensity and carrying capacity. Patchy breeding distributions will tend to increase spatial heterogeneity in population density, whereas dispersal from breeding patches will tend to decrease it. The potential for dispersal to homogenize densities is likely to differ both among organisms (e.g. plants vs. mobile animals) and throughout ontogeny (e.g. larvae vs. adults). However, for mobile organisms, experimental studies of the importance of breeding distributions from the wild are largely lacking.

2. In the present study, experimental manipulations replicated over eight natural streams and 2 years enabled us to test for effects of the distribution of Atlantic salmon eggs over spatial scales which are relevant to local interactions among individuals. Artificial nests were placed along 250 m study reaches at one of two levels of nest dispersion – patchy (two nests per stream) and dispersed (10 nests per stream) – while holding total egg density (eggs m^{-2} stream area) constant.

3. Nest dispersion had significant effects on the spatial distribution of the resulting juveniles in their first summer. Patchy nest distributions resulted in a highly right-skewed frequency distribution of local under-yearling densities (among 25 m sampling sections), as sample sections adjacent to the nest sites had relatively high densities. In contrast, dispersed nest distributions yielded approximately normal density distributions. Sections with high relative densities in the patchy nest distribution treatments also had relatively small juvenile body sizes, and patchy egg distribution appeared to produce a higher redistribution of individuals from the first to the second juvenile growth season than the dispersed distribution.

4. Because patchy breeding distribution combined with limited early dispersal can create spatial variation in density over scales directly relevant for individual interactions, this will be one important component in determining mean levels of early juvenile competition and its spatial variation within populations. Assuming random or ideal-free distribution of individuals may therefore underestimate the mean level of density experienced by juveniles over surprisingly small spatial scales (orders of magnitude smaller than total spatial extent of populations), even for mobile organisms.

Key-words: carrying capacity, density dependence, population regulation, spatial structure, *Salmo salar.*

Introduction

Small-scale spatial variation in density can have important implications for population and recruitment dynamics. In

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plants and other sessile organisms, the intensity of density-dependent processes such as intraspecific competition is determined largely by local interactions among neighbouring individuals (e.g. Ramseier & Weiner 2006). One important source of their local spatial variation in density is the spatial distribution of breeding adults, resulting in an aggregated

Table 1. Study streams characteristics and details on the stocking of Atlantic salmon eggs (total number per year and number of nests among which the eggs were distributed) during 2 years in the River Conon system

Stream	Sub-catchment	Wet width	Eggs year^{-1}	Nests 2005	Nests 2006
1. Coire a Bhuic	Meig	4·5	5625	2	10
2. Glen Meinnich	Meig	4·6	5750	10	2
3. Scardroy Burn	Meig	4·9	6125	10	2
4. Inchbae Burn	Blackwater	4·3	5375	2	10
5. Allt a Choire Ghorblach	Blackwater	3·8	4750	10	2
6. Marksie Burn	Upper Conon	3·6	4500	2	10
7. Allt Caiseachain	Bran	3·6	4500	10	2
8. Distillery Burn	Conon	3·6	4500	10	2

distribution around these (Nathan & Muller-Landau 2000), which may influence strongly subsequent juvenile recruitment (Harms *et al.* 2000; Wright *et al.* 2005). The importance of local-scale variation in density has been recognized increasingly even for mobile animals (Folt & Schulze 1993; Pfister & Peacor 2003; Wilkin *et al.* 2006). However, the effect of the spatial distribution of breeding adults has received much less attention in these species.

Among mobile organisms, the importance of spatial breeding distribution may be particularly important for highly fecund species with small initial size. In such species, if dispersal involves active individual movements (as opposed to passive drift), bioenergetic constraints on dispersal are likely to be initially strong, but decreasing with increasing age (Roff 1991). This, combined with a rapidly declining risk of mortality with age (Dahlberg 1979), suggests that mobility should be restricted initially but increase throughout ontogeny. According to this hypothesis, two predictions can be made. First, if early mobility is restricted, differences in breeding distribution patterns among populations should be detectable in the spatial distribution of early juveniles. Secondly, if mobility increases with age, redistribution of individuals will be directly proportional to the degree of initial clumping, and will break down spatial correlations between density of juveniles from a given cohort measured at two different sampling occasions. The strength of such correlations should therefore decrease with increased patchiness in the egg distribution.

Breeding dispersion and juvenile dispersal abilities may be particularly important in shaping the population dynamics of stream-dwelling salmonid fishes. Salmonids build discrete nests, where they deposit 100s to 1000s of eggs. Both restricted physical habitat requirements for spawning (Armstrong *et al.* 2003) and maps showing spatial distributions of salmonid nests (Geist & Dauble 1998; Moir *et al.* 2004; Isaak & Thurow 2006) indicate that salmonid breeding may commonly be patchy on a 10–100 m scale. Dispersion of breeding sites may therefore influence density-dependent population processes through effects on variation in local juvenile densities. However, it is not known whether the particular arrangement of nests on such small spatial scales translates into variation in juvenile densities and, if it does, how this variation persists throughout ontogeny.

The biology of salmon (i.e. lack of extended parental care, high fecundity, discrete nests and easy production of fertilized

eggs which are tolerant to mechanical disturbance during late developmental stages) also makes this taxon particularly suited for experimental studies of effects of breeding distribution. In the present study the effects of breeding distribution were tested over a scale where spatial considerations are commonly ignored in salmonid population studies. The spatial distribution of Atlantic salmon (*Salmo salar* L.) nests was manipulated over 250 m reaches (approximately two orders of magnitude smaller than typical salmon streams), replicated over eight streams and 2 years, and the resulting patterns of juvenile densities were examined. We tested the specific hypothesis that patchy breeding distributions will result in different spatial distributions of juveniles compared to dispersed breeding distributions, and examined whether patterns of spatial redistribution were consistent with an ontogenetic increase in mobility.

Materials and methods

STUDY SITES AND EGG STOCKING

Ten small tributaries to the River Conon, Ross-shire, Northern Scotland, all being located above migration barriers which prevented natural spawning by salmon, were used initially in this study. Two of the streams proved unsuitable for salmon production (few or no surviving juveniles were recovered) and were hence excluded. In each stream one 250 m reach with suitable juvenile habitat based on water depths, substrate and current velocities was identified (Fig. 1a, Table 1). Atlantic salmon eggs were obtained from wild adults caught in a fish trap on the River Blackwater during November 2004, and these were fertilized and incubated in the Scottish Hydro-electric hatchery at Contin. Eggs from 16 family groups were mixed in a common hatchery tray, and the streams were stocked using these between 24 February and 3 March 2005. Stocking densities were held constant at five eggs m^{-2} in the different streams (based on measured winter wet widths) over the 250 m reach, but with two different outplanting strategies (Table 1, Fig. 1b). In three of the eight streams which were included in the study the eggs were divided equally between two nests located 250 m apart ('patchy' distribution), whereas in the remaining five streams the eggs were divided equally between 10 nests located 28 m apart ('dispersed' distribution). Each nest was created by digging a pit in the gravel bed, and Vibert boxes (Federation of Fly Fishermen, Bozeman, MT, USA) containing the eggs were placed within the pit before being covered with gravel. The outplanting was repeated in a similar way during
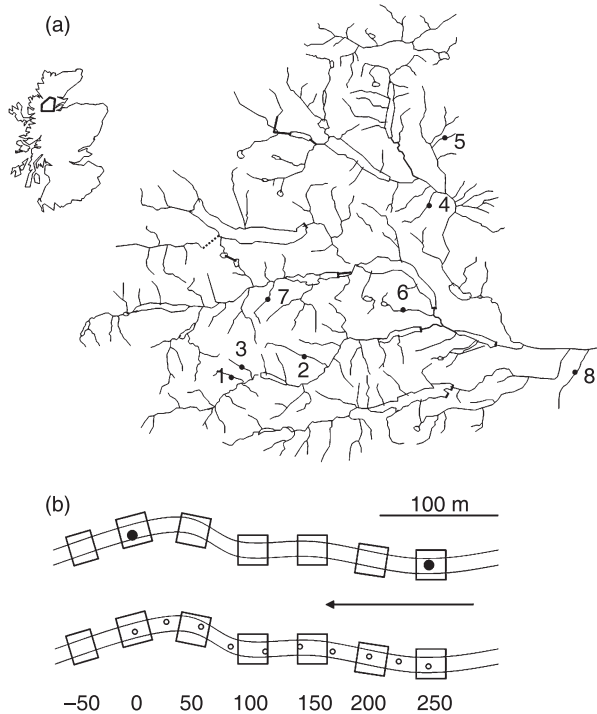
Fig. 1. (a) Map of the River Conon and its location. Stream reaches used for egg stocking are numbered according to Table 1. (b) Outline of study design, representing a single stream in 2 consecutive years (two-nest outplanting treatment in upper version, and 10-nest treatment in lower version). Circles represent nests, squares represent sections for recapture sampling and arrow indicates direction of water flow.

23 February – 2 March in 2006, using eggs from a mixed batch of 16 family groups originating from adults caught in the River Blackwater during November 2005, but with the treatments swapped such that streams that received the eggs in two nests the previous year now received 10 nests, and vice versa.

JUVENILE SAMPLING

During the periods 11–20 July 2005 and 12–30 July 2006 the streams were electrofished to obtain data on spatial distributions and sizes of juveniles. Seven stream sections were sampled by a single electro-fishing pass in all streams in both years, with most of the sections being 25 m long (some were shorter due to the presence of pool habitats not suitable for under-yearling juveniles). The centre of these sections were located at –50, 0, 50, 100, 150, 200 and 250 m relative to the lowermost nest site, with the negative sign indicating down-stream direction and positive sign upstream (Fig. 1b). Some of the streams had waterfalls preventing migration upstream of the 250 m section, and the present design was therefore chosen to allow an equal sampling distribution among sites. All caught salmon were measured for length, and their age (under-yearling, 1 year or older) determined by size distributions. At the completion of a section the fish were put into enclosures placed within the section in which they were captured, and then re-released later in the stream.

The single pass method cannot be used to estimate the actual numbers of fish present in a given section, compared with the multiple pass approach (e.g. Bohlin *et al.* 1989), but provides data on variation in fish abundance among sampling sections that contain some noise due to variation in catchability. This approach was chosen because the multiple pass approach performs poorly (large confidence inter-vals) in sections containing few fish (Bohlin *et al.* 1989), as was expected with the current outplanting and sampling design. Fur-thermore, we conducted multiple passes in one to two sections of each stream and year that yielded more than 10 under-yearlings in the first pass. Catchabilities estimated by the modified Zippin pro-cedure (Bohlin *et al.* 1989) based on these data suggested that a sin-gle pass caught, on average, 67% of the under-yearlings present, and that noise due to variation in catchability was relatively low (mean catchability = 0·67, SD = 0·08, $n = 19$). Finally, because we were interested only in the relative spatial distribution among the stream sections between the two treatments, we normalized density data for each stream and year by taking the difference between the section-specific observation and the stream-year average and dividing this by the standard deviation of observations among sections for that stream-year. This removes variation in the data caused by differ-ences in both overall survival and catchability among streams and between years. To enable examination of how variation in relative density among stream sections influenced relative body size, mean body sizes for each section were normalized in the same way.

Results

Manipulation of egg distribution patterns produced clear differences in the spatial distribution of under-yearling salmon juveniles. We detected a significant interaction between section and nest treatment (patchy vs. dispersed) on density of under-yearling salmon ($F = 2·36$, d.f. = 6, 98, $P = 0·036$, Fig. 2). Specifically, going upstream from the –50 section, there was a more or less continuous, gradual decrease in densities in the dispersed treatments. As a result, there was a significant spatial autocorrelation in normalized densities in this treatment (density in each section against density in the section above, $n = 6$, $r = 0·83$, $P = 0·042$). In contrast, in the patchy nest treatments, there was a decrease in density at
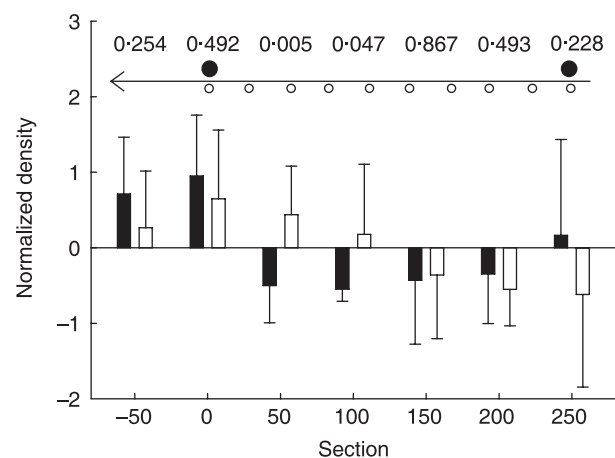

Fig. 2. Mean (± 1 SD) normalized density of juvenile under-yearling salmon in different stream sections when eggs were outplanted in two (closed bars) and 10 nests (open bars). Arrow indicates direction of water flow, and nest locations are indicated by closed (two-nest treatments) and open circles (10-nest treatments). *P*-values for ANOVA comparisons of densities between the two treatments are indicated for each stream section.
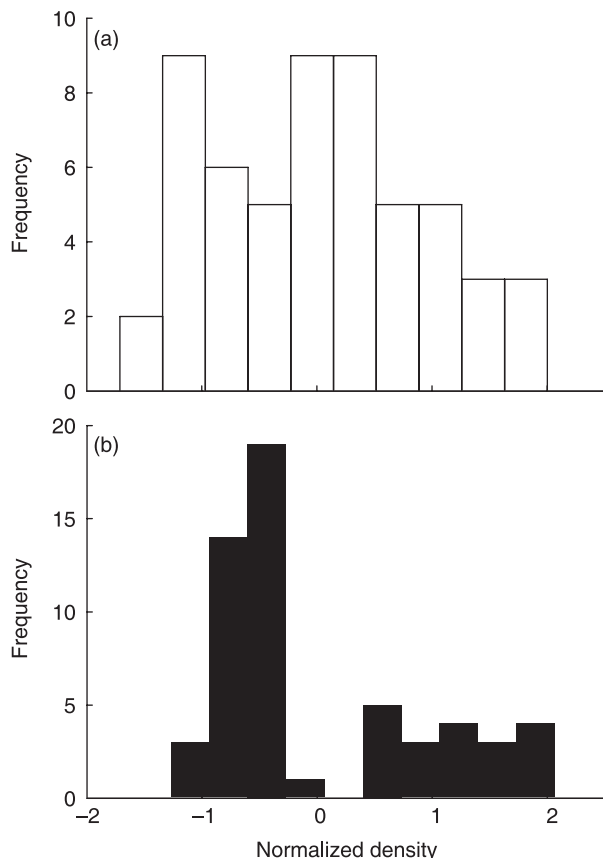
Fig. 3. Frequency distributions of normalized density of juvenile under-yearling salmon in different stream sections when eggs were outplanted in (a) 10 and (b) two nests.
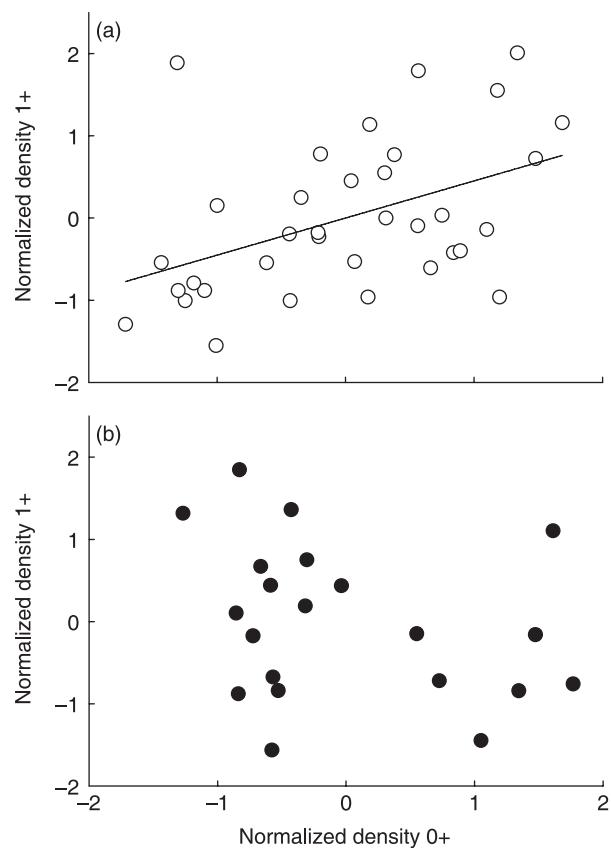

Fig. 4. Relationship between density of under-yearling salmon and the corresponding density of 1-year-old fish the following year among stream sections for (a) the 10-nest [1 year = 0·00 (0·14 SE) + 0·45 (0·16 SE) under-yearling, $n = 35$, $r^2 = 0·20$, $P = 0·007$] and (b) the two-nest treatment [1 year = 0·00 (0·20 SE) – 0·30 (0·22 SE) under-yearling, $n = 21$, $r^2 = 0·09$, $P = 0·192$].

the first section upstream of the lowermost nest (Fig. 2), and no spatial autocorrelation ($n = 6$, $r = 0·40$, $P = 0·434$). Furthermore, *post-hoc* ANOVAS demonstrated a significantly lower relative density in the two- than in the 10-nest treatment at the 50 m section (Fig. 2). The same was true even when comparing absolute densities in this section (mean densities 0·19 vs. 0·42 ind. m^{-2}, pairwise *t*-test, $t = 3·19$, d.f. = 7, $P = 0·015$), but not in the other sections (all *P*-values > 0·1). However, these analyses of absolute densities may be influenced to some extent by annual variation in survival rates, which could not be controlled for with the present design, and should therefore be treated more cautiously. The deficiency of juveniles just above the lowermost nest in the two-nest treatment suggests successful dispersal from nests to occur predominantly in the downstream direction. This is also indicated by the gradual increase in density when going downstream in the 10-nest treatment, suggesting that juveniles originating from an increasing number of nests are present. The two different treatments also resulted in significantly different frequency distributions of normalized under-yearling densities (two-sample Kolmogorov–Smirnov test, $n = 112$, $Z = 1·42$, $P = 0·036$). The 10-nest treatment resulted in a distribution of densities that closely approximated a normal distribution (Kolmogorov–Smirnov test for deviation from normal distribution, $n = 56$, $Z = 0·52$, $P = 0·947$, Fig. 3a). In contrast, the two-nest treatment had a high frequency of low-density

sections, a pronounced tail towards high densities and, as a result, differed significantly from a normal distribution (Kolmogorov–Smirnov, $n = 56$, $Z = 1·94$, $P = 0·001$, Fig. 3b).

To test whether the distribution of eggs also influenced patterns of net movement among sections over the period from the first to the second sampling, we plotted the normalized density of under-yearlings for the different sections in 2005 against the normalized density of 1-year-olds the following year. In the 10-nest treatment, there was a highly significant positive correlation between these two measures (Fig. 4a). Thus, in this treatment, a high density of under-yearlings resulted in a corresponding high density of 1-year-olds the following year. In contrast, within the two-nest treatment, no significant correlation was observed (Fig. 4b).

To test directly whether the divergence in spatial distribution of under-yearling densities influenced the relative spatial distribution of body sizes, we first calculated the difference in normalized density between the two treatments for each section and stream, and similarly the difference in normalized body size. These were closely negatively correlated (Fig. 5). Thus, sections that had high relative densities in the two-nest treatment compared to those in the 10-nest treatment also had a relatively small juvenile body size, and vice versa.
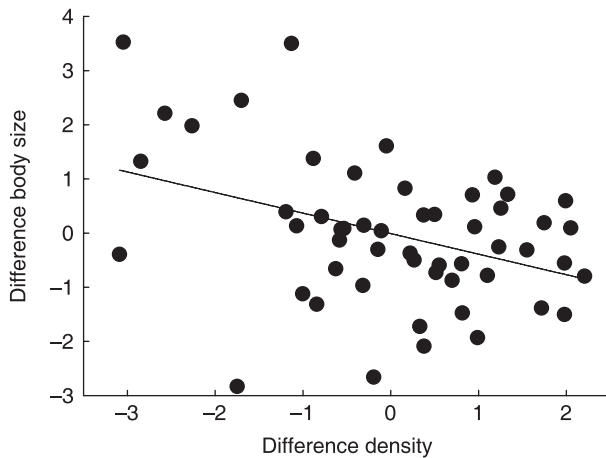
Fig. 5. Relationship between mean difference in under-yearling Atlantic salmon normalized density between two- and 10-nest treatments for different sections and streams and corresponding difference in normalized body size. Positive values indicate higher relative density (*x*-axis) and body size (*y*-axis) in a given section and stream for the two-nest treatment than for the 10-nest treatment. Difference size = 0·03 (0·17 SE) – 0·40 (0·13 SE) difference density, $n = 53$, $r^2 = 0.15$, $P = 0.004$.

Discussion

Field experiments replicated over eight separate streams and 2 years gave support to the hypothesis that breeding distributions can have important effects on the spatial variation in juvenile densities over scales relevant for individual interactions, but which are commonly ignored in salmonid population studies. Nest dispersion (patchy vs. dispersed) over 250-m long stream reaches influenced the spatial distribution of the resulting juveniles in their first summer. Patchy distributions resulted in a highly right-skewed distribution of local densities, as sample sections adjacent to the nest sites had relatively high densities. In contrast, dispersed nest distributions yielded approximately normal density distributions. Sections that had high relative densities in the two-nest treatment compared to that in the 10-nest treatment also had a relatively small juvenile body size, and vice versa, suggesting that such small-scale patterns in breeding distributions may also influence juvenile performance through density-dependent effects.

The observed temporal correlations between under-yearling and 1-year-old individuals were consistent with the patchy egg distribution producing a higher redistribution of individuals from the first to the second juvenile growth season than the dispersed distribution. This is also consistent with mobility in juvenile Atlantic salmon being initially restricted and increasing with age. Ontogenetic changes in juvenile salmonid mobility have been inferred previously from descriptive quantifications of the spatial distribution of different development stages (Beall *et al.* 1994; Webb *et al.* 2001; Johnsen & Hvidsten 2002). In addition, more direct tests using field experiments have shown that high local density causes increased mortality during the early juvenile stage (i.e. fry at onset of exogenous feeding; Einum & Nislow 2005), whereas local density has no effect on mortality but strong effects on dispersal when juveniles are released at an older stage (i.e. 2–3 months after onset of feeding; Einum, Sundt-Hansen & Nislow 2006). Einum *et al.* (2006) suggested that these results demonstrate how ontogenetic changes in the way density-dependent effects are partitioned among survival, growth and dispersal occur in correlation with changes in individual mortality risks and dispersal abilities. However, this conclusion was based partly on the response of individuals which had been hatchery-reared and outplanted at predetermined densities as older juveniles. Hatchery rearing can alter behavioural traits (reviewed in Einum & Fleming 2001), and density manipulations at older juvenile stages may create situations that are rare or absent in natural populations if regulation of local densities occur at an earlier life stage. Moreover, such manipulations may exclude the effects of post-settlement site fidelity, which can be important in naturally developing populations (Armstrong, Shackley & Gardiner 1994). The present study therefore complements these previous studies, suggesting that those patterns identified in more controlled experimental situations can also be important in natural populations.

Although spatial ecology has received much attention during the last few decades, most of the recent theoretical efforts have focused upon metapopulation ecology (reviewed by Hanski 1999). A wide range of organisms living in more or less continuous habitats may experience small-scale spatial structure without qualifying as meta-populations (Freckleton & Watkinson 2002). Recent inclusion of spatial structure in continuous space, discrete-time (i.e. Ricker model; Travis 2003) and continuous-time models (i.e. logistic model; Law, Murrell & Dieckmann 2003) suggest that such structuring can have non-trivial effects on population dynamics. Important population parameters determining the effect of spatial structure include neighbourhood size (i.e. area surrounding an individual within which other individuals influence its fitness) and dispersal distance. Both these parameters, and perhaps particularly neighbourhood size, are difficult to estimate in the wild (Travis 2003), and as a result empirical work examining the role of spatial structure of mobile organisms in continuous habitats remains rare.

For salmonid populations we are just beginning to understand how important spatial structuring may be for population dynamics. Limited mobility and hence probably also relatively small neighbourhood sizes following emergence from nests is predicted to have strong effects on important characteristics such as population growth rates, equilibrium size and stability (Travis 2003), and such effects will be augmented by their patchy egg distribution. Given the small scale over which the spatial distribution of juvenile densities and performance has been linked to breeding distribution (present study; Einum & Nislow 2005) and the large scale of typical salmon rivers (e.g. Norwegian rivers: mean 21·1 km, median 11·5 km, $n = 156$; L'Abée-Lund, Vøllestad & Beldring 2004), it seems likely that the distribution of breeders can have pronounced effects on spatial competitive heterogeneity, and hence population carrying capacity. Future empirical work

on small-scale spatial structure and its effects on population dynamics will probably contribute to a more detailed understanding of ecological processes in salmonids. Thus far, one may conclude that assuming random or ideal-free distribution of individuals (e.g. mean-field approximation, Hiebeler 2000) will tend to underestimate the mean level of density experienced by early juveniles over surprisingly small spatial scales. This is also probably the case for other mobile organisms in which patchy breeding distributions and limitations to dispersal during early life stages can cause spatial population structure (e.g. insects, Ray & Hastings 1996).

Acknowledgements

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